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Ice-related seasonality in zooplankton community composition in a high Arctic fjord

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Seasonal mesozooplankton community composition was studied monthly from March to October 2007 in the high Arctic, Rijpfjorden (Svalbard), and related to abiotic (hydrography, sea ice) and biotic (ice algae and phytoplankton biomass) environmental conditions. The community was numerically dominated by the cosmopolitan *Oithona similis*, whereas Arctic *Calanus glacialis* was the dominant taxon in terms of biomass. Seasonal mesozooplankton community development was largely influenced by the sea ice and hydrographic conditions, which impacted the primary production regime in the fjord. Three distinct periods could be identified based on species and life stages composition: (i) winter–spring transition (March–June), with high ice algal biomass in April–June, characterized by peak abundances of *Pseudocalanus minutus*, *Calanus glacialis* females and *Clione limacina*; (ii) sea ice break-up and phytoplankton bloom (July), with high numbers of *Calanus* nauplii and young copepodids, as well as larvae of benthic crustaceans such as Cirripedia and Decapoda; and (iii) ice-free post-bloom period (August–October), when the pulse of warm waters into the fjord resulted in development of a community with Atlantic characteristics and peak abundances of *Oithona similis*, *Oithona atlantica*, *Limacina helicina* and Echinodermata larvae within the upper 50 m. At the same time, older copepodids of *Calanus glacialis* and *Calanus finmarchicus* had already descended to overwintering depths (>100 m). Despite the 2–3 months delay in

the phytoplankton bloom compared with ice-free Svalbard fjords, the Rjippfjorden mesozooplankton managed to fulfill their life cycles in a similar time, likely due to the utilization of the ice algal bloom, and warmer water enhancing species growth and development in late summer.

KEYWORDS: mesozooplankton; *Calanus*; Rjippfjorden; seasonal succession; sea ice

INTRODUCTION

A limited number of studies have followed the seasonal zooplankton development over an annual cycle in the high Arctic (Richter, 1995; Arashkevich *et al.*, 2002). In Svalbard, seasonal zooplankton investigations have taken place mainly in Kongsfjorden, a fjord located on the west coast of Spitsbergen (79°N, 12°E), which is strongly influenced by relatively warm Atlantic waters and thus limited or no sea ice has formed there during the last decade (Svendsen *et al.*, 2002; Cottier *et al.*, 2005; Walkusz *et al.*, 2009). Arnkværn *et al.* (Arnkværn *et al.*, 2005) investigated the seasonal population dynamics of the copepods *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in Billefjorden (78°40'N), which is a sill-fjord at the very end of the larger Isfjorden system. Many studies in the Svalbard area have focused on *Calanus* species, due to their importance in the Arctic ecosystems and the possible influence of warming on them (Søreide *et al.*, 2010; Carstensen *et al.*, 2012). Time-series of the zooplankton community seasonal development are available from Kongsfjorden and Rjippfjorden, from sediment traps deployed on moorings that have been operating in these two fjords since 2002 and 2006, respectively (Willis *et al.*, 2006, 2008; Berge *et al.*, 2009; Wallace *et al.*, 2010).

The observations from Kongsfjorden revealed significant differences among seasons, with generally lower total zooplankton abundances in spring and increasing numbers toward autumn, observed both in the net and sediment trap samples (Willis *et al.*, 2006; Walkusz *et al.*, 2009). In spring, zooplankton in the net samples was dominated by Cirripedia nauplii (Walkusz *et al.*, 2009), and generally data from the sediment trap confirm the trends seen in the net data, although with higher temporary resolution (Willis *et al.*, 2006). In June, after the peak of the phytoplankton bloom, zooplankton collected in the sediment traps was dominated by young development stages, while during autumn, increased abundances were recorded of *Oithona similis* and *Microcalanus* sp. as well as overwintering *Calanus* stages (Willis *et al.*, 2006; Walkusz *et al.*, 2009). The authors also argued that advection was the main factor shaping the zooplankton community in Kongsfjorden, and that hydrological drivers override the importance of local biological processes in this system.

Rjippfjorden (80°N, 22°30'E) is a north-facing fjord, situated on Nordaustlandet, and open toward the Arctic Ocean. Due to its high-Arctic location, the fjord is usually covered by fast ice in winter–spring (Berge *et al.*, 2009). Because of the limited influence of advected warm Atlantic water into the fjord, its zooplankton community is dominated mainly by true Arctic species (Falk-Petersen *et al.*, 2008). During the study in Rjippfjorden in 2007, parallel to the present mesozooplankton community study, the seasonal development of algal blooms was also studied (Leu *et al.*, 2010, 2011).

The aim of this study was to investigate how seasonal changes in environmental conditions such as the presence of sea ice and ice algal and phytoplankton blooms, as well as changes in hydrographic properties of the water, influence the composition, vertical distribution and seasonal development of mesozooplankton in Rjippfjorden, a fjord in high-latitude Arctic. It was the first study that allowed us to collect zooplankton samples, along with hydrological and environmental data, systematically from March to October, at monthly intervals, from a location so far north in the European Arctic.

METHOD

Hydrology, ice conditions and blooms

Temperature, salinity and *in situ* fluorescence were measured by instruments mounted on a mooring placed close to the sampling station. In addition to the continuous mooring data, we measured salinity, temperature and *in situ* fluorescence each time after collecting zooplankton samples, apart from September. From March to July, these measurements were made with a handheld CTD equipped with a fluorometer (MiniSTD model SD-204, SAIV AS, Bergen, Norway), while from August to October, they were obtained using a Sea-Bird Electronics SBE 911+ CTD (for details, see Søreide *et al.*, 2010 and Leu *et al.*, 2011).

Zooplankton sample collection and analysis

The zooplankton sampling station (SH) was established close to the mooring, in the outer fjord basin (80°

15.954 N; 22° 17.397 E, bottom depth: 148 m) (Fig. 1). Zooplankton samples were collected in Rippfjorden each month from March to October 2007. Initially, four sets of samples (March–June) were taken after making a hole in the ice. In July, the sampling was conducted in open water from a small boat and in the following months (August–October), zooplankton samples were collected from larger research vessels (Table I).

Stratified vertical net hauls were performed using either a WP2 closing net with 200 μm mesh size (150 μm mesh size in March) or a MultiNet (HYDRO-BIOS©, Kiel, Germany) consisting of four nets with a 0.25 m^2 opening and 200 μm mesh size. The depth strata sampled were: 0–20, 20–50, 50–100 m and 100–bottom. The lower

limit of the deepest layer sampled was set a few meters off the sea bottom. The maximum depth was usually ~ 140 m, apart from September, when, the deepest haul was taken from 186 m. Due to the large differences in sampling depths in the deepest layer between September and other months, all data were proportionally calculated as if the layer thickness was 40 m.

Zooplankton samples were preserved in 4% buffered formaldehyde in seawater, immediately after sampling. Organisms were identified and counted under a stereomicroscope equipped with an ocular micrometer, following standard procedures (Harris *et al.*, 2000). Most of the copepods were identified to species or genus level, and copepodid developmental stages were also

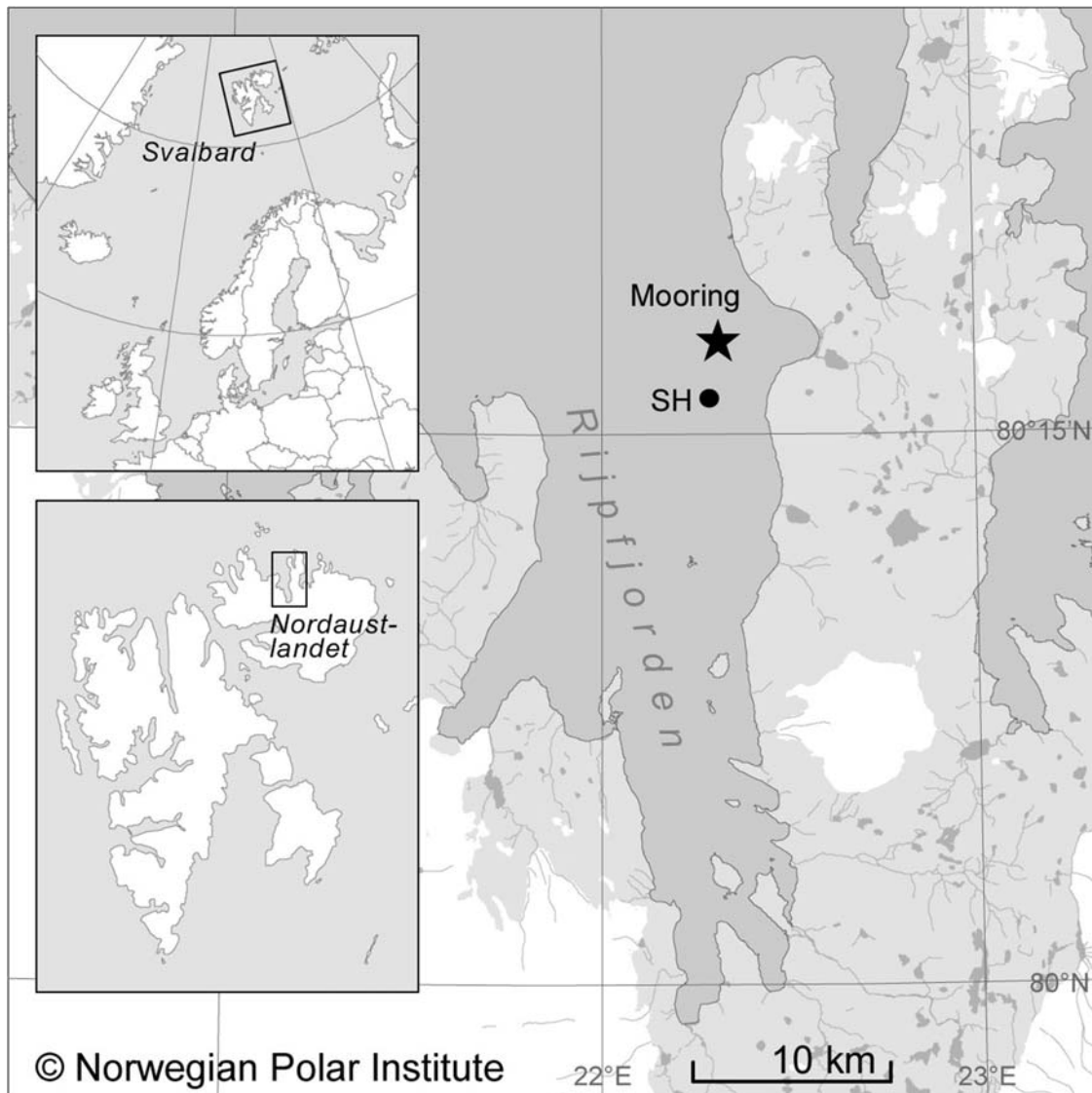


Fig. 1. Rippfjorden, showing the locations of the sampling station (SH) and the mooring.

Table I: Overview of zooplankton samples collected from March to October 2007 in Rjippfjorden at Stn. SH (Fig. 1)

Date	Layer (m)	Net type/ mesh size	Platform
06.03.2007	0–20, 20–50, 50–100, 100–140	WP2/150	Ice
23.04.2007	0–20, 20–50, 50–100, 100–145	WP2/200	Ice
01.05.2007	0–20, 20–50, 50–100, 100–140	WP2/200	Ice
05.06.2007	0–20, 20–50, 50–100, 100–140	WP2/200	Ice
16.07.2007	0–20, 20–50, 50–100, 100–140	WP2/200	Boat
22.08.2007	0–20, 20–50, 50–100, 100–140	MPS/200	JM
04.09.2007	0–20, 20–50, 50–100, 100–186	MPS/200	JM
07.10.2007	0–20, 20–50, 50–100, 100–130	MPS/200	Lance

The samples were collected from these platforms: a hole in the sea ice (Ice) from March to June, from a small boat (Boat) in July and from the larger research vessels “Jan Mayen” (JM) and “Lance” in August, September and October.

identified for larger copepods that were sampled effectively (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa* and *Pseudocalanus*). To identify *Calanus* species, prosome length was measured following the procedure in Weydmann and Kwaśniewski (Weydmann and Kwaśniewski, 2008). Biomass was calculated from abundance data and individual dry mass (DM) values according to (Blachowiak-Samolyk *et al.*, 2008).

Statistical analyses

To study the relationship between abiotic (sampling depth, temperature, salinity, ice thickness and the date of sample collection) and biotic (sea ice algae and phytoplankton chlorophyll *a* biomass) environmental variables and meso-zooplankton community composition, constrained ordination techniques were applied in the CANOCO for Windows v4.5 software (ter Braak and Smilauer, 2002). Redundancy analysis (RDA) was based on depth-specific abundances of species and their life stages (ind. m⁻³) for the depth layers: 0–20, 20–50, 50–100 and 100–140 m, which were set as a split-plot design. Zooplankton abundance data were log-transformed [$x' = \log(x + 1)$] prior to analyses to meet the requirements of normal distribution and to allow assessment of the possible influence of numerically less important taxa. The environmental variables were ranked, according to their quantitative importance, by manual selection based on the Monte Carlo permutation test adjusted for temporal autocorrelation (ter Braak and Smilauer, 2002).

Significance tests for differences between separated groups of samples, identified by the RDA, were performed using a one-way ANOSIM (analysis of similarities) permutation test. While SIMPER (similarity percentages) analysis was used to decompose, average Bray–Curtis

dissimilarities between the groups distinguished, and to determine the contribution of each species to the within-groups similarity. Both analyses were run on the log-transformed data of species and stage abundances (ind. m⁻³) in order to reduce the influence of the most common taxa, using PRIMER version 6.0 (Plymouth Marine Laboratory, Plymouth, UK) (Clarke and Warwick, 1994). For the purpose of both PRIMER and CANOCO analyses, larval stages of numerically less important taxa, such as Gastropoda veligers and larvae, or Cirripedia nauplii and cypris, were grouped together as Gastropoda and Cirripedia larvae, respectively.

RESULTS

Hydrology, ice conditions and timing of algal blooms

In autumn 2006, an influx of warmer water into Rjippfjorden was observed (Wallace *et al.*, 2010). The fjord froze in early February 2007 and was completely covered by landfast ice, with a thickness of ~1 m, until the end of June. At the beginning of July, the sea ice started to break up, and by 12 July, the fjord was ice-free (Leu *et al.*, 2010; Søreide *et al.*, 2010). During the period of ice-cover, the water column was homogenous with a temperature close to freezing (–1.7 to –1.9°C) and constant salinity (34.3–34.8) (Wallace *et al.*, 2010). In July, the ice broke up and melted, which resulted in water column stratification. The highest temperature (2.5–3.3°C) and the lowest salinity were recorded in the upper 50 m in July and August (Leu *et al.*, 2010, 2011; Søreide *et al.*, 2010; Wallace *et al.*, 2010).

Between March and October, there were two main distinct algal blooms, corresponding with two peaks in polyunsaturated fatty acids production: in April and July. The ice algal bloom started in mid-end of April and lasted until the middle of June. An intensive phytoplankton bloom was observed after ice breakup in late June/beginning of July (Leu *et al.*, 2010, 2011; Søreide *et al.*, 2010).

Zooplankton community and its seasonal changes

A total number of 42 taxa were recorded in Rjippfjorden from March to October in 2007 (Table II). The most common were two *Calanus* species (*C. finmarchicus* and *C. glacialis*) as well as *Oithona similis* and *Pseudocalanus* spp. Most of the taxa recorded were present in all seasons and throughout the entire water column, although their abundance and biomass greatly varied among months

Table II: Taxa recorded in Rijpfjorden in 2007, minimum and maximum abundance (ind. m⁻²) and biomass (mg DM m⁻²), and month with maximum biomass and abundance (Month)

Species	Abundance (ind. m ⁻²)		Biomass (mg DM m ⁻²)		Month of maximum abundance/biomass
	Min	Max	Min	Max	
<i>Calanus finmarchicus</i>	1257	51 865	169.6	7691.5	September
<i>Calanus glacialis</i>	962	44 333	607.6	12 701.1	September
<i>Calanus hyperboreus</i>	16	2744	7.6	579.0	July
<i>Microcalanus spp.</i>	133	4622	0.9	32.4	October
<i>Pseudocalanus spp.</i>	5947	63 679	37.1	304.7	September
<i>P. acuspes</i> females	0	4058	0	52.9	September
<i>P. minutus</i> females	116	1312	1.7	38.4	June
<i>Metridia longa</i>	0	953	0.0	141.9	March
<i>Acartia longiremis</i>	13	1067	0.2	12.9	October
<i>Microsetella norvegica</i>	0	12	n.d.	n.d.	August
<i>Oithona atlantica</i>	0	315	0.0	2.2	October
<i>Oithona similis</i>	9326	256 189	23.1	641.4	October
<i>Triconia (= Oncaea) borealis</i>	0	1183	0.0	2.4	October
<i>Oncaea</i> spp.	0	180	0.0	0.4	March
<i>Calanus nauplii</i>	111	34 016	0.5	206.0	July
<i>Discoconchoecia elegans</i>	0	39	0.0	2.6	October
<i>Cirripedia nauplii</i>	0	742	0.0	15.6	July
<i>Cirripedia cypris</i>	0	266	0.0	5.6	July
<i>Themisto abyssorum</i>	0	4	0.0	0.5	May/July/ August
<i>Themisto libellula</i>	0	17	0.0	21.1	June/July
<i>Isopoda</i> indet.	4	58	0.0	16.0	June
<i>Thyssanoessa longicaudata</i>	0	12	0.0	5.4	October
<i>Euphausiacea nauplii</i>	0	204	n.d.	n.d.	July
<i>Euphausiacea calyptopis</i>	0	16	0.0	11.0	July
<i>Eupagurus zoea</i>	0	36	n.d.	n.d.	July
<i>Hyas zoea</i>	0	52	n.d.	n.d.	July
<i>Pandalus borealis zoea</i>	0	4	n.d.	n.d.	July
<i>Sabinea septemcarinata zoea</i>	0	4	0.0	3.8	June
<i>Bougainvillea</i> spp.	0	20	n.d.	n.d.	May/June
<i>Sarsia</i> sp.	0	24	n.d.	n.d.	June
<i>Beroë cucumis</i>	6	72	3.3	40.3	June
<i>Mertensia ovum</i>	0	27	n.d.	n.d.	October
<i>Clione limacina</i>	13	184	8.9	106.4	March
<i>Limacina helicina</i>	32	2093	4.3	376.5	October
<i>L. retroversa</i>	0	200	n.d.	n.d.	September
Gastropoda veliger (cf. <i>Velutina</i>)	0	80	0.0	145.5	July

Continued

Table II: Continued

Gastropoda veliger	0	24	0.0	0.1	May
Gastropoda larvae	4	40 428	0.0	19.5	September
Polychaeta indet.	4	421	0.0	2.1	August
Echinodermata larvae	0	36 933	0.0	604.9	August
<i>Eukrohnia hamata</i>	0	10 825	0.0	22.3	August
<i>Parasagitta elegans</i>	86	932	1.4	194.0	September
<i>Fritillaria borealis</i>	0	5189	0.0	4.1	October
<i>Oikopleura</i> spp.	4	4168	0.0	277.0	August

and depths. The maximum abundance (ind. m⁻²) and biomass (DM mg m⁻²) of the species identified coincided in time (Table III).

Mesozooplankton abundance and biomass varied over the seasons with a well-marked differences among the winter–spring ice covered period from March to June which included the ice algal bloom, the open water season in summer with the phytoplankton bloom (July) and the post-bloom season (August–October) (Fig. 2). The highest values of total zooplankton abundance (426 200 ind. m⁻²) and biomass (22.3 g DM m⁻²) were found in September, when most taxa had their peak abundance and biomass, while the lowest abundance (18 460 ind. m⁻²) and biomass (0.9 g DM m⁻²) were noted in April (Table II, Fig. 2).

Oithona similis was, at all times, the most abundant species, reaching up to 256 000 ind. m⁻² in October (Fig. 2). The second most abundant taxon was *Pseudocalanus* spp. (up to 63 680 ind. m⁻² in March), apart from June and July when *Calanus* nauplii dominated with 34 020 ind. m⁻² in July, and except for August when Echinodermata larvae were particularly abundant (36 930 ind. m⁻²). Pelagic larvae of benthic crustaceans such as Cirripedia and Decapoda, as well as the larvae of Euphausiacea, occurred in relatively high numbers in July during the phytoplankton bloom (Table II). With respect to biomass, the most important species during the entire study period was *C. glacialis*, which reached up to 12.7 g DM m⁻² in September (Fig. 2). Its sibling species, *C. finmarchicus*, was the second most important species in this respect, with a maximum of 7.7 g DM m⁻², also in September. Considering non-copepod taxa, gastropods were the most important, with the biomass of *Limacina helicina* up to 0.4 g DM m⁻² in August (Table II).

Vertical distribution

Vertical distribution patterns of individual taxa, as well as of the entire mesozooplankton community, varied

strongly among seasons (Fig. 3). In late winter (March), the mesozooplankton community abundance ranged from 490 ind. m⁻³ (20–50 m) to 1330 ind. m⁻³ (0–20 m) with no clear increase or decrease in abundance with depth. The distribution of biomass was more or less similar throughout the water column, with a peak due to *C. glacialis* in 50–100 m layer (22 mg DM m⁻³).

During the maximum ice algal growth season (from April to June), total mesozooplankton abundance was generally lower than in March. The highest numbers were recorded in upper water layers: 380 and 760 ind. m⁻³ in 0–20 m in April and June, respectively, and 380 ind. m⁻³ in 20–50 m in May, all caused by

relatively high abundances of *O. similis* and *Pseudocalanus* spp. During the winter–spring transition, zooplankton abundance generally decreased with depth. The biomass was also low during these months, apart from the surface layer in June, where 74 mg DM m⁻³ was recorded mostly due to *C. glacialis* (60.5 mg DM m⁻³). During the phytoplankton bloom in July, with a chlorophyll *a* peak ~40 m (Søreide *et al.*, 2010), the highest abundance and biomass (3240 ind. m⁻³ and 60 mg DM m⁻³, respectively) were recorded between 20 and 50 m depth. During this period, the peak of abundance was caused by *Calanus* nauplii (1060 ind. m⁻³), *C. finmarchicus* (690 ind. m⁻³) and Echinodermata larvae (650 ind. m⁻³), whereas the peak in biomass was mostly due to *C. glacialis* (42.6 mg DM m⁻³) (Fig. 3).

Over the entire study period, the highest abundances were recorded in the surface water layers in August, September and October, with the overall maximum of 5970 ind. m⁻³ in 0–20 m layer in September. This was the result of extremely high numbers of *O. similis*. In September, high numbers of gastropods, mainly *Limacina helicina*, were also observed in a sub-surface layer (780 ind. m⁻³ in 20–50 m). During these months, the zooplankton attained high biomass, with the peak of 326 mg DM m⁻³ in the bottom layer in September, due to the high numbers of older stages of *C. glacialis*

Table III: Environmental variables (conditional effects) that best explained the variability of mesozooplankton community in Røypfjorden 2007

Variable	Variance explained (%)	P-value	F-value
Ice thickness	27	0.022	10.95
Chlorophyll <i>a</i>	9	0.006	4.25
Temperature	7	0.010	3.30
Salinity	6	0.050	3.08
Total	48.7		

These variables are significant, according to the Monte Carlo permutation test.

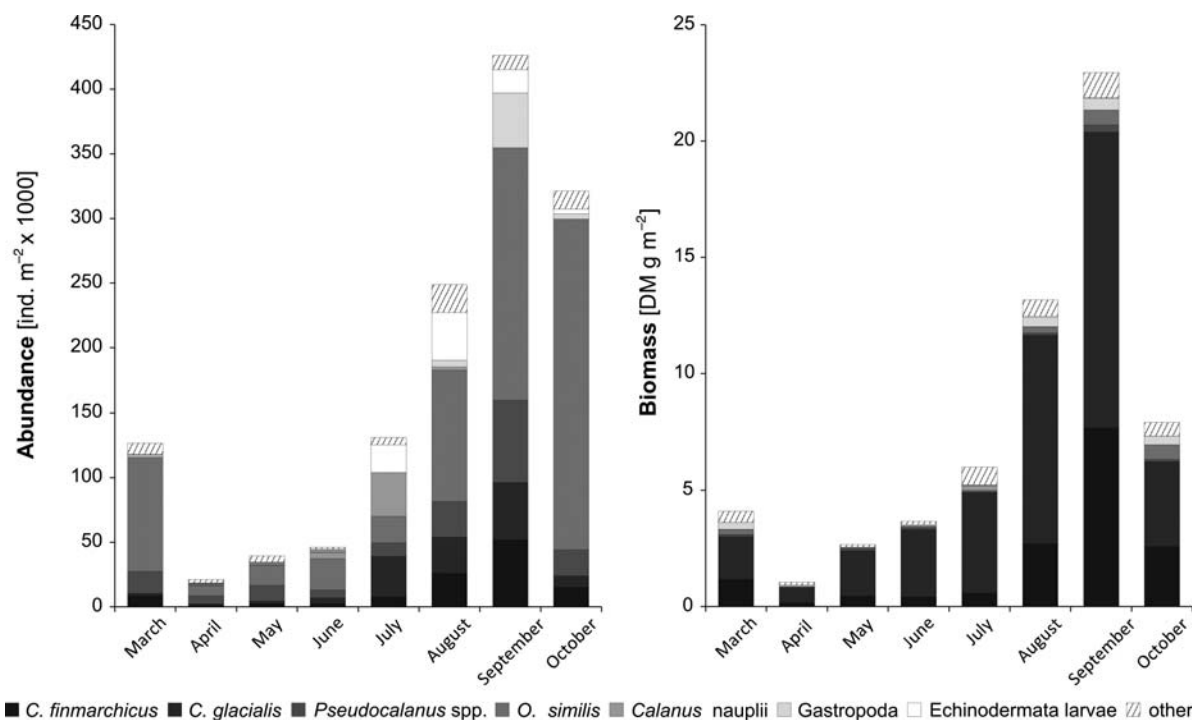


Fig. 2. Abundance (ind. m⁻²) and biomass (DM g m⁻²) of the main mesozooplankton taxa in subsequent months.

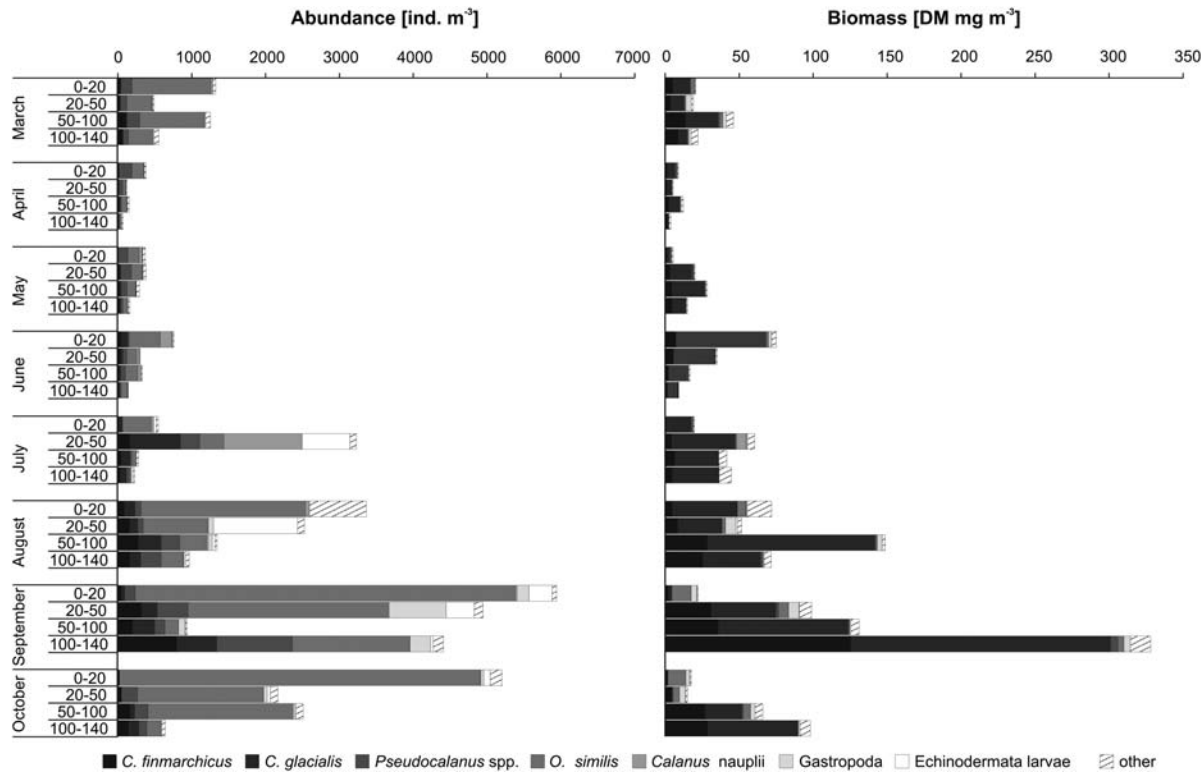


Fig. 3. Vertical scheme of abundance (ind. m^{-3}) and biomass (DM mg m^{-3}) of the main mesozooplankton taxa in Rjippfjorden from March to October 2007.

(175 mg DM m^{-3}) and *C. finmarchicus* (125 mg DM m^{-3}) (Fig. 3).

Influence of environmental factors on the zooplankton community

The model based on the species–environment relationship in the RDA ($P = 0.001$) succeeded in explaining half (48.7%) of the total observed variability in zooplankton composition and abundance in Rjippfjorden from March to October (Table III). The environmental variable that had largest explanatory power was sea ice thickness, which alone explained 27% of the total mesozooplankton variability. In addition to the variability explained by sea ice thickness, chlorophyll *a* (m^{-3}) explained the remaining 9% of the zooplankton variability, followed by the mean temperature (7%) and salinity (6%) (Table III).

The RDA analysis revealed both the importance of ice cover in the fjord and zooplankton community seasonal cycle over the observation period (Fig. 4). The major part of zooplankton variability was closely related to sea ice thickness and water temperature, both responsible for the ordering of the samples along the first canonical axis, which explained 31.9% of the species–

environment relationship. An additional 10.5% of the total zooplankton variability was closely correlated with chlorophyll *a*, which is expressed by the relation of this factor eigenvector with the second axis of the RDA plot (Fig. 4).

During the winter–spring transition (March–June), the fjord was covered by sea ice ($\sim 1 \text{ m}$ thick), with high ice algal biomass from late April to June (Leu *et al.*, 2010). In association with this, high abundances of *C. glacialis* and *Pseudocalanus minutus* females, as well as *Clione limacina* were observed (Fig. 4). The similarity of the community composition in this period, as well as the importance of ice cover, is illustrated by the winter and spring samples clustering closely together in the RDA plot, and the association of the ice thickness variable marker with the cluster. New developmental stages of the year, such as *Calanus* nauplii, Cirripedia larvae and *Hyas* sp. zoea, were recorded in highest numbers during the peak phytoplankton biomass in July. In the subsequent months (August–October), with the pulse of warmer water advected from the outer shelf, the temperature of the surface and subsurface layers in the fjord increased (Fig. 1 in Soreide *et al.*, 2010), young copepodid stages (CI–CIII) of *Calanus* spp., *O. similis*, *Fritillaria borealis* as well as *L. helicina*, Echinodermata

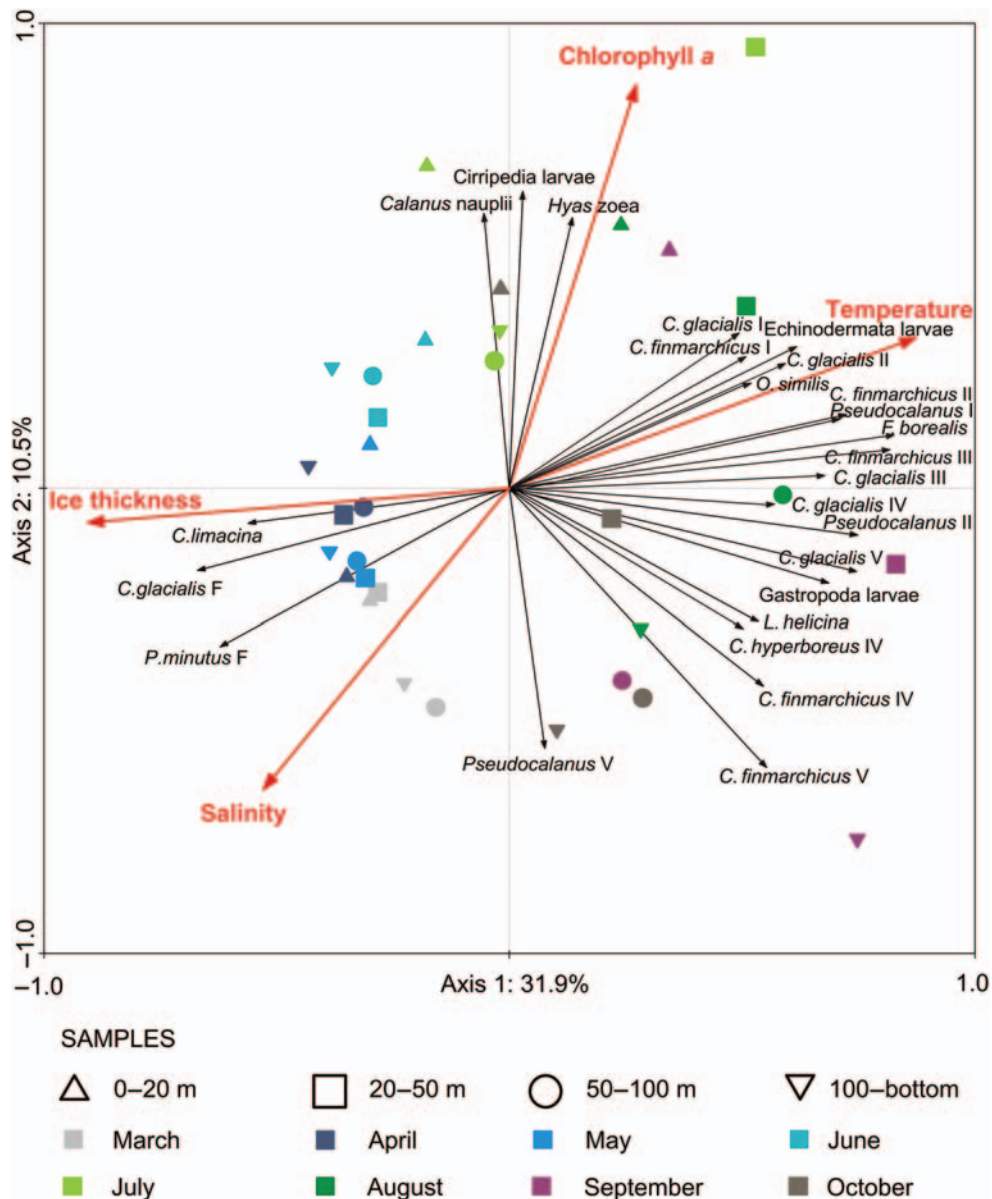


Fig. 4. Ordination of samples by RDA in respect of mesozooplankton abundance and its relation to environmental variables (red arrows). The plot shows the 27 best fitted taxa (black arrows). The proportions of the total variability explained by the first two axes are given.

and Gastropoda larvae were found in high numbers. At the same time, but in deeper layers, the older copepodid stages (CIV–CV) of *Calanus* spp. and *Pseudocalanus* spp. were abundant (Fig. 4).

Seasonal changes in community structure

One-way ANOSIM revealed significant differences in the zooplankton community composition among (i) winter–spring transition, when the fjord was covered by sea ice (WINTER–SPRING, March–June); (ii) summer

(July) during the phytoplankton bloom (BLOOM); and (iii) during the post bloom (POST-BLOOM) period in August–October autumn (global $R = 0.788$, $P = 0.001$). The SIMPER analysis revealed average dissimilarities in mesozooplankton community composition between the groups from 49.4% (BLOOM and POST-BLOOM) to 56.4% (WINTER–SPRING and BLOOM, Table IV). Except for *O. similis*, which was numerous during the entire year, the following taxa contributed mostly to similarities within the periods indicated and were characteristic for the seasons: *Microcalanus* spp.,

Table IV: The results of pairwise tests between defined groups and SIMPER analysis comparing the average dissimilarity (%) between the groups

Groups	ANOSIM		SIMPER Average dissimilarity (%)
	R	P-value	
WINTER–SPRING, BLOOM	0.862	0.001	56.42
WINTER–SPRING, POST-BLOOM	0.814	0.001	52.37
BLOOM, POST-BLOOM	0.626	0.002	49.36

R, ANOSIM statistics for tests; P, significance level.

and *P. minutus* females of WINTER–SPRING; *C. glacialis* CIII–CV and *Calanus* spp. nauplii of BLOOM, and *C. finmarchicus* CV, and *Pseudocalanus* spp. CII–CIII, and Gastropoda larvae of the POST-BLOOM group (Table V). Echinodermata larvae were typical for both BLOOM and POST-BLOOM periods, while *Pseudocalanus* spp. CIV–CV and *C. finmarchicus* CIV were characteristic for WINTER–SPRING and POST-BLOOM seasons.

DISCUSSION

The mesozooplankton community and its seasonal development in Rjippfjorden was largely impacted by the prevailing sea ice conditions, which in turn influenced hydrography and the primary production regime in the fjord. During the winter–spring transition period, from March to June, the community was dominated numerically by Arctic species, while in autumn, the advection of relatively warm water masses resulted in the community composition being more dominated by Atlantic taxa. We can assume that from February, when the sea ice formed, to July, changes in the Rjippfjorden mesozooplankton community were mainly due to seasonal succession of local populations caused by species mortality, development and reproduction. In contrast, the changes in mesozooplankton community composition in the post-bloom period were largely due to the influx of Atlantic taxa from the shelf outside Rjippfjorden.

Winter–spring transition

From March to June, Rjippfjorden was covered by land fast sea ice of ~1 m thickness, which led to the formation of cold, homogenous water masses throughout the whole water column. The mesozooplankton abundance and biomass was low and dominated by copepods, mainly *Calanus glacialis* and *Pseudocalanus* spp.,

Table V: SIMPER list of taxa contributing mostly to similarities within the following periods, with a cut-off at 50%

Taxon	Average similarity	Contribution (%)	Cumulative contribution (%)
WINTER–SPRING: average similarity 65.02%			
<i>O. similis</i>	11.54	17.75	17.75
<i>Pseudocalanus</i> spp. CV	6.01	9.24	26.99
<i>Microcalanus</i> spp.	5.39	8.29	35.28
<i>Pseudocalanus</i> spp. CIV	4.62	7.10	42.39
<i>C. finmarchicus</i> CIV	4.41	6.78	49.17
<i>P. minutus</i> F	3.95	6.08	55.24
BLOOM: average similarity 53.60%			
<i>O. similis</i>	6.48	12.09	12.09
<i>C. glacialis</i> CIV	5.70	10.64	22.74
<i>Calanus</i> nauplii	4.99	9.31	32.05
Echinodermata larvae	4.33	8.09	40.13
<i>C. glacialis</i> CV	4.33	8.07	48.20
<i>C. glacialis</i> CIII	3.60	6.72	54.92
POST-BLOOM: average similarity 65.49%			
<i>O. similis</i>	8.29	12.65	12.65
<i>C. finmarchicus</i> CIV	3.72	5.68	18.33
<i>C. finmarchicus</i> CV	3.44	5.26	23.59
<i>Pseudocalanus</i> spp. CII	3.42	5.21	28.80
<i>Pseudocalanus</i> spp. CIII	3.32	5.07	33.87
<i>Pseudocalanus</i> spp. CIV	3.27	4.99	38.86
Echinodermata larvae	3.10	4.74	43.60
<i>Pseudocalanus</i> spp. CV	3.07	4.69	48.29
Gastropoda larvae	3.01	4.60	52.89

represented by their overwintering stages and females about to begin reproduction, as well by Arctic species such as *Clione limacina*, which reflects the natural state of the zooplankton community at the beginning of a new production season. Low zooplankton numbers and similar copepod stage composition during the winter–spring transition have also been observed in the other Svalbard fjords, such as Kongsfjorden (Willis *et al.*, 2008; Walkusz *et al.*, 2009) and Hornsund (Węslawski *et al.*, 1991).

Ice algae, growing on the under-surface of the ice, and being released during ice melt, constitute a fundamental food source, especially for females of Arctic species during their reproduction (Tourangeau and Runge, 1991; Søreide *et al.*, 2010). *Pseudocalanus minutus* and *C. glacialis* females respond to seasonal melting of sea ice and release of the ice algae into the water column, by migrating to the surface layers to feed, while

completing gonad maturation (Runge and Ingram, 1991; Falk-Petersen *et al.*, 2007; Runge *et al.*, 2007). Such close associations of reproducing females of *C. glacialis* and *Pseudocalanus* spp. with higher ice concentrations were well captured by the RDA model and by SIMPER analysis.

June was the month of transition between the ice-covered and ice-free fjord, and higher levels of chlorophyll *a* in the surface water layer at this time were most likely caused by the ice algae sloughed off the underside of the ice when the ice started to break up (Leu *et al.*, 2011). *Calanus* nauplii and young stages (CI and CII) of *C. glacialis* started to appear at this time of the year, particularly in the surface layer, although females and CIV were still the most numerous. This was similar to the observation by Hop *et al.* (Hop *et al.*, 2011), who noted dense concentrations of *C. glacialis* associated with meltwater in the Amundsen Gulf (Arctic Canada). During the same time, in the deeper waters in Rippfjorden, zooplankton composition and abundance were similar to those observed in the previous period, indicating that the community was still not in its spring developmental phase.

Phytoplankton bloom

July was the period of the most dramatic changes in Rippfjorden with the ice break-up and subsequent intensive phytoplankton bloom with a chlorophyll *a* peak ~40 m (Søreide *et al.*, 2010; Leu *et al.*, 2011), and consequently, peaks in zooplankton abundance and biomass were recorded in the sub-surface layer. High densities of young stages of copepods: *Calanus* nauplii, *Calanus finmarchicus*, *C. glacialis* and *Pseudocalanus* spp. were found, most likely actively feeding as described by other authors (Eilertsen *et al.*, 1989; Scott *et al.*, 2000; Søreide *et al.*, 2010). Also the larvae of Cirripedia, Echinodermata and *Hyas* sp. were observed in the chlorophyll *a* maximum layer, possibly taking advantage of the phytoplankton bloom. Similarly, the increased numbers of Echinodermata larvae were also observed in Kongsfjorden by the end of July by Walkusz *et al.* (Walkusz *et al.*, 2009). However, the zooplankton were scarce in the uppermost part of the water column, probably due to the fresh water observed because of the sea ice melting and river run-off (Søreide *et al.*, 2010; Leu *et al.*, 2011). Increased abundance of female *Pseudocalanus acuspes* found in June suggests that this species started to reproduce during the phytoplankton bloom in July. This observation is consistent with findings by Conover and Huntley (Conover and Huntley, 1991) who observed that *P. acuspes* started growth at the beginning of the pelagic bloom, reaching sexual maturity at the ice breakup or slightly before.

The long-lasting sea ice cover delayed the phytoplankton bloom in Rippfjorden compared with Kongsfjorden by ~2–3 months (Rokkan Iversen and Seuthe, 2011; Hodal *et al.*, 2012). The seasonal succession of the mesozooplankton community, however, seemed to be delayed by ~1–2 months in the more Arctic fjord depending on the species (Willis *et al.*, 2006; Walkusz *et al.*, 2009). For example, peak concentrations of young *Calanus* copepodids (CI–CII) and pelagic larvae of Cirripedia were found in early July in Rippfjorden and May–June in Kongsfjorden (Willis *et al.*, 2006; Søreide *et al.*, 2010). Possible explanation of the shorter delay in development of zooplankton, compared with phytoplankton, may be the fact that in Rippfjorden, zooplankton could feed on ice algae and therefore they could start feeding prior to the appearance of the phytoplankton bloom. The onset of the ice algal bloom in Rippfjorden occurred roughly at the same time as the onset of phytoplankton in Kongsfjorden (Leu *et al.*, 2006; Rokkan Iversen and Seuthe, 2011; Hodal *et al.*, 2012) and other fjords on West Spitsbergen (Zajaczkowski *et al.*, 2010; Sorensen *et al.*, 2012). In Rippfjorden, the ice algae may have been first easily accessible for zooplankton when the sea ice started to melt. In June, the increasing chlorophyll *a* concentrations in the upper 5 m in Rippfjorden were caused by ice algae being sloughed off the underside of the melting ice (Leu *et al.*, 2010). Therefore, the stage composition of the key copepods in June–July in Rippfjorden and the presence of large numbers of *Calanus* nauplii were comparable to those observed in Kongsfjorden in April–May (Willis *et al.*, 2006; Walkusz *et al.*, 2009). On the other hand, the first appearance of *C. finmarchicus* young stages (CI–CIII) in Rippfjorden occurred 1 month later (July versus June) than in Billefjorden (Arnkværn *et al.*, 2005) and much later than in the Norwegian Sea (Hirche *et al.*, 2001).

Post-bloom period

The influx of warm water masses from the shelf areas north of Rippfjorden in July 2007 was observed shortly after the sea ice breakup. At the same time, the zooplankton community in Rippfjorden changed to a dominance of younger copepodid stages of *Calanus* spp. and *Pseudocalanus* spp., as well as larval stages of *Limacina* spp. The warm water influx also coincided with the increase in Atlantic species such as *C. finmarchicus*, *Oithona atlantica*, *Fritillaria borealis* and *L. helicina* in Rippfjorden and it also led to favorable conditions for the further development of pelagic primary and secondary production (Leu *et al.*, 2011).

In the course of the post bloom-period, zooplankton was characterized by high numbers of the overwintering stages of *C. finmarchicus*, *C. glacialis* and *Pseudocalanus* spp., which migrated toward deeper parts of the water column in September and October, likely to overwinter after having accumulated sufficient energy reserves (Conover and Huntley, 1991; Scott *et al.*, 2000). However, zooplankton abundance in the deepest layer from September could have been slightly overestimated as the result of deeper sampling due to a ship's drift. Similar stage composition during autumn was observed in Kongsfjorden (Willis *et al.*, 2006; Walkusz *et al.*, 2009) and in Billefjorden (Arnkvaern *et al.*, 2005). Such a scenario of *Calanus* seasonal development was also proposed for Rijpfjorden by Falk-Petersen *et al.* (Falk-Petersen *et al.*, 2008), who found that three *Calanus* species numerically dominated the zooplankton community in this fjord in September 2004. Due to the seasonal succession of the zooplankton community, although with some differences in timing resulting from specific Arctic conditions in Rijpfjorden, all species managed to reach overwintering stages in autumn, as they do in the other Svalbard fjords.

Concluding remarks

Three similar phases in the seasonal progress in composition and abundance of mesozooplankton have also been found in Kongsfjorden (Willis *et al.*, 2006; Walkusz *et al.*, 2009), which resembles a sub-Arctic rather than a high-Arctic fjord and is not impacted by sea ice (Svendsen *et al.*, 2002; Cottier *et al.*, 2005). Rijpfjorden has an extensive seasonal sea ice cover with an ice break-up normally in June–July (Ambrose *et al.*, 2006; Leu *et al.*, 2011). Most mesozooplankton species at high-Arctic latitudes have minimum a 1-year life cycle (Arnkvaern *et al.*, 2005; Weydmann and Kwasniewski, 2008). Despite a 2–3 months delay in the onset of the phytoplankton spring bloom in Rijpfjorden compared with ice-free fjords of Svalbard, the seasonal mesozooplankton development in Rijpfjorden was not similarly delayed in time. The likely reason for this was the high ice algal biomass present from late April to June, which fueled reproduction of key Arctic grazers such as *C. glacialis* and *Pseudocalanus* spp. (Søreide *et al.*, 2010). Until this time, the changes in mesozooplankton community composition were driven mainly by the natural processes connected with mortality, development and reproduction. However, the combination of high phytoplankton biomass and increasing seawater temperatures after July accelerated mesozooplankton growth and developmental time, making it possible for populations in Rijpfjorden to fulfill their life cycles in 1 year and thus match the seasonal mesozooplankton development in ice-free Svalbard fjords.

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